

# PTERYGOTE INSECTS AND THE SOIL: THEIR DIVERSITY, THEIR EFFECTS ON SOILS AND THE PROBLEM OF SPECIES IDENTIFICATION

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## ABSTRACT

Attention is focussed on soil-dwelling pterygote insects that directly influence soil profiles and soil fabrics, especially on the largest order of insects the Coleoptera or beetles, and is then further restricted to groups that are important in the tropics and in the southern hemisphere. This means especially termites (Isoptera) and ants (Hymenoptera, Formicidae). These two groups of insects affect soil structure by building mounds and excavating nest chambers and galleries, often raising lower horizon material to the surface. They also influence the nature of organic matter and its distribution in the soil profile and, consequently, the horizontal dispersion of plant nutrients. Some of these influences are illustrated by reference to recent work on the micromorphological and profile-forming effects of termites. Recent Australian studies are also used to illustrate the pedological effects of ants. In turn, Australian ants introduce, and are used to exemplify, the general taxonomic problem presented by many groups of soil-associated pterygote insects in many parts of the world: numerous species, most of which are underscribed. The magnitude of this problem is examined on a world basis and it is suggested that the conventional taxonomic process should be inverted: work should proceed downward, starting from the higher taxa, organizing the species of larger genera in natural species groups. Species-level taxonomic studies can be deferred, carried out on a provisional basis or concentrated on critical groups of species.

## RÉSUMÉ

L'auteur passe en revue les groupes d'insectes ptérygotes qui habitent le sol et autres habitats semblables. Il se concentre sur ceux qui influencent directement les horizons et la structure des sols, plus particulièrement sur les Coléoptères, qui forment le plus grand ordre d'insectes; par la suite il restreint encore davantage son analyses aux groupes importants des tropiques et de l'hémisphère sud, c'est-à-dire plus spécialement les termites (Isoptères) et les fourmis (Hyménoptères, Formicidae). Ces deux groupes d'insectes affectent la structure du sol en construisant des monticules et en creusant des chambres de reproduction et des galeries, amenant ainsi à la surface des matières provenant des horizons inférieurs. Ils influencent aussi la nature de la matière organique et sa répartition dans le profil du sol et, par conséquent, la dispersion horizontale des éléments nutritifs des plantes. Quelques-uns de ces effets sont illustrés à l'aide d'exemples de travaux récents sur le mode d'influence des termites sur la micromorphologie et la formation du profil des sols. De récentes études australiennes servent aussi d'exemples pour illustrer les effets des fourmis sur les sols. De même, l'exemple des fourmis australiennes sert à illustrer le problème général d'ordre taxonomique que présentent plusieurs groupes d'insectes ptérygotes associés aux sols dans plusieurs régions du monde, c'est-à-dire la présence d'un très grand nombre d'espèces dont la grande majorité n'est pas décrite. L'auteur analyse l'ampleur de ce problème à l'échelle mondiale et conclut que le processus conventionnel de la taxonomie devrait être inversé: c'est-à-dire que les travaux devraient progresser du général au particulier, en étudiant d'abord les taxons supérieurs et en divisant les gros genres en groupements naturels d'espèces. Quant aux traitements taxonomiques des espèces, ils peuvent être soit retardés, soit exécutés de façon provisoire, ou encore concentrés sur des groupes d'espèces

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*critiques.*

## INTRODUCTION

The subclass Pterygota consists of insects which, as adults, are winged or are secondarily apterous. The subclass contains about three-quarters of all the described species of animals and a very substantial proportion of them are associated with the soil system. This refers to the actual mineral and organic horizons of the soil profile and also to related decomposition habitats such as decaying wood and fallen fruits, carrion and dung. Conventionally regarded as soil animals as well are those that are active on the soil surface, among insects for example, many carabid beetles and ants. Indeed it is at the air-soil interface *i.e.*, the soil surface and uppermost part of the soil profile, that biological activity and diversity usually reach their absolute maxima in terrestrial ecosystems. Much of this diversity, both taxonomic diversity and diversity of form and function, is due to pterygote insects. This account of pterygote-soil relationships is inevitably cursory, even with several restrictions of the area which I attempt to cover. In accordance with the subject of the Symposium, attention is concentrated on those pterygote groups that influence soil fabrics and the constitution of soil profiles. Until recent years, by far the greater part of research in soil zoology had been carried out in temperate regions in the northern hemisphere. Here, therefore, as a gesture towards restoring some balance, and to complement other contributions to this volume, I emphasize two groups, termites and ants, that are particularly important in soils throughout the tropics and over much of the southern hemisphere. I also select out the Coleoptera or beetles, by far the largest order of insects and whose species interact with the soil in a multitude of different ways.

## THE VARIETY OF SOIL PTERYGOTA

Of the 26 orders that form the Pterygota all but seven contain at least some species in which an active life history stage involves or depends directly on the soil system. The Phasmatodea (stick insects) live and feed on vegetation (although the eggs are deposited on or laid in the soil), while Phthiraptera (lice), Siphonaptera (fleas) and Strepsiptera are parasitic. Three other orders have winged, generally short-lived adults and exclusively aquatic larvae. Similarly the Odonata (Dragonflies) and Trichoptera (caddisflies) are essentially aquatic but in both groups are a few species with truly terrestrial larvae living, for example, in rainforest litter far from standing water. Increasing terrestriality is seen in the Mecoptera (scorpion flies); the larvae are mainly aquatic or are found in damp swampy habitats but some are predators and scavengers on the open soil surface and in litter.

The other 16 orders are of varying importance in the soil system. Zorapterans, grylloblattodeans, and embiopterans are relatively small and obscure orders and are, as a rule, of minor functional importance. Zorapterans are small (length < 3mm) gregarious insects living in logs in the tropics. Grylloblattodeans are small and are found under stones and logs, and in the soil in cold wet situations in the northern hemisphere. The mainly tropical embiopterans construct silken galleries, sometimes in leaf litter, under stones or in crevices in the soil. Mantodea (preying mantises) are primarily predators on vegetation but there are some representatives adapted to life on the soil surface.

Members of all the remaining dozen orders contribute significantly to soil processes. The Isoptera (termites) are the most closely associated with the soil and they, with the ants (Hymenoptera, Formicidae, are dealt with separately below. The activities and influences of

the rest of the Pterygota are far too varied for it to be possible here to do more than note a few salient points for most orders.

Blattodeans (cockroaches) and dermapterans (earwigs) are omnivorous feeders and detritivores. Ground-living psocopterans (booklice) and thysanopterans (thrips) feed on a wide range of unicellular algae, lichens and fungal hyphae and spores amongst litter and on the soil surface. Orthoptera (grasshoppers and crickets) include many cryptic forms that shelter in burrows in soil and decaying wood or under debris, and a smaller number of wholly subterranean species that are highly adapted morphologically to life in the soil (Key, 1970). Among the Neuroptera (lace wings) there are families whose larvae are terrestrial predators, notably the ant-lions (Myremeleontidae) some of which construct pitfall traps in loose sandy soils. The importance of Lepidoptera (butterflies and moths) as soil animals is probably underestimated. In Australia the larvae of at least six families, especially Tortricidae, feed on dead leaves in the litter layer, (Common, 1970), very often when the dry condition of these leaves inhibits attack or decomposition by other organisms, while some cossid larvae feed, internally or externally, on the roots of trees and shrubs. Ground-living Hemiptera (bugs) include seed-feeders, a wide variety of predators and fungus feeders. Some aphids and, probably, most cydnidas are root-feeders. The Diptera (flies) form one of the larger orders of insects and very many of their larvae occur in moist, nutrient-rich habitats such as decaying fruits, dung, rotting vegetation, carrion and logs which have a large active microbial population at a moderately advanced stage of decomposition. Some of these larvae are predaceous and many others have more or less specialised relationships with fungi.

A more detailed examination of the remaining order, the Coleoptera (beetles), which contains about 40% of all known insect species and perhaps a third, or even more, of all animal species, illustrates the taxonomic complexity of pterygotes associated with the soil. In Table 1 the families of Coleoptera are arranged in four groups. Group 1 consists of families composed of species that can be regarded as effectively independent of the soil both as adults and larvae. It covers parasites, aquatic forms, species living entirely on vegetation or in the nests of vertebrates and social insects. Group 2 includes all families that have representatives functioning in the soil system, including species whose activities are centred on discrete habitat units such as logs and vertebrate dung and carrion. Group 3 excludes the latter and is restricted to families with species living in soil or litter or on the soil surface. Group 4 is further restricted to families containing species that penetrate the soil profile and are therefore likely to affect soil properties directly. Table 1 is derived from a summary of the classification of Coleoptera given by Britton (1970) modified according to subsequent major changes (Britton, 1974). This classification is essentially that of Crowson (1955, 1967) and it was used also by Richards and Davies (1960) who provide brief notes on the biology of the families. Several points should be noted. The Table refers to species of Coleoptera known in 1970. By 1974 the total had risen from about 280,000 species to 290,000 (Britton, 1974). If this represents a steady rate of increase, the total should now stand at around 320,000 known species. However this must still fall very far short of the real total of all species of Coleoptera (see below). Inevitably the attribution to categories 1-4 in the Table is arbitrary and debatable for many taxa. Families are placed according to whether they contain representatives in the habitat groups 1-4. The Carabidae for example are in Group 4 because the family contains species with burrowing adults while the larvae of many species with surface-active adults live in the upper part of the soil profile. This does not mean however that all Carabidae fall in Group 4 and indeed there are many highly adapted arboreal carabid species, especially in tropical rain-forests. It does mean

TABLE 1. Degree of association of families of Coleoptera with soil and allied habitats. The Table shows the number of known species in families which contain representatives variously associated with the soil. Only the major families (> 2,000 known species) are shown individually; the fractions represent number of families/number of known species (see text).

Superfamily	Habitat				Totals
	1	2	3	4	
Family	Unrelated to soil (or uncertain)	Soil System	Ground layer	Soil profile	
Cupedoidea	—	2/26	—	—	2/26
Sphaeroidea	4/22	—	—	—	4/22
Caraboidea					8/30,184
Carabidae	—	1/25,000	1/25,000	1/25,000	
Other families	6/5,059	1/125	—	—	
Hydrophiloidea					5/2,400
Hydrophilidae	—	1/2,000	—	—	
Other families	4/400	—	—	—	
Histeroidea					3/2,507
Histeridae	—	1/2,500	—	—	
Other families	—	2/7	—	—	
Staphylinoidea					10/35,149
Staphylinidae	—	1/27,000	1/27,000	—	
Pselaphidae	—	1/5,000	1/5,000	—	
Other families	3/49	5/3,100	4/2,800	—	
Scarabaeoidea					6/18,827
Scarabaeidae	—	1/17,000	1/17,000	1/17,000	
Other families	—	5/1,287	3/1,587	1/300	
Eucinetoidae	1/360	2/85	1/61	—	3/445
Dascilloidea	1/50	2/69	2/69	1/65	3/119
Byrrhoidea	—	2/300	1/270	—	2/300
Dryopoidea	7/1,008	—	—	—	7/1,008
Buprestoidea					1/11,500
Buprestidae	—	1/11,500	—	—	
Artemetopidea	1/45	2/115	1/1	—	3/160
Elateroidea					5/8,208
Elateridae	—	1/7,000	1/7,000	1/7,000	
Other families	—	4/1,208	1/3	—	
Cantharoidea					7/8,252
Lycidae	—	1/3,000	1/3,000	1/3,000	
Cantharidae	—	1/3,500	1/3,500	—	
Other families	1/3	4/1,749	4/1,749	—	
Dermestoidea	3/88	1/731	—	—	4/819

(continued on next page)

Table 1 (continued)

Superfamily	Habitat				Totals
	1	2	3	4	
Family	Unrelated to soil (or uncertain)	Soil System	Ground layer	Soil profile	
Bostrychoidea	1/700	3/1,604	1/70	1/70	4/2,304
Cleroidea					7/9,152
Cleridae	–	1/3,400	–	–	
Melyridae	–	1/4,000	1/4,000	1/4,000	
Other families	1/3	4/1,749	4/1,749	–	
Lymexyloidea	–	1/37	–	–	1/37
Cucujoidea					46/41,011
Nitidulidae	–	1/2,200	1/2,200	–	
Coccinellidae	1/5,000	–	–	–	
Meloidea	1/2,000	–	–	–	
Tenebrionidae	–	1/16,100	1/16,100	–	
Other families	16/2,702	26/13,009	8/8,087	–	
Chrysomeloidea					3/41,200
Cerambycidae	–	1/20,000	1/20,000	1/20,000	
Chrysomelidae	–	1/20,000	1/20,000	1/20,000	
Other families	1/1,200	–	–	–	
Curculionoidea					8/61,264
Anthribidae	–	1/2,400	–	–	
Curculionidae	–	1/60,000	1/60,000	1/60,000	
Other families	4/514	2/1,350	–	1/1,060	
Totals	56/19,200	86/258,621	43/225,857	12/137,495	142/282,880

that identification of a carabid species from soil entails its discrimination within a family of more than 20,000 known species.

The functional complexity of soil-associated Coleoptera has to be considered as well. The very high proportion of families in Group 2 in Table 1, and the large number of known species in these families (over a quarter of a million) reflects, in part, the close association of Coleoptera with dead wood and fungi. For example, many Coleoptera have mycangia, structures that allow adult beetles to transport fungal spores when they move from one site to another. The superfamily Cucujoidea is particularly well represented in Group 2. It is conservatively divided into 45 families but well over 50 can be recognised, ranging from the Tenebrionidae, a major family of important detritivores, especially in the tropics and

TABLE 2. Summary of the superfamily Scarabaeoidea (Coleoptera): larval habitats and food

Family Subfamily	Known species (1970)	Larval habitat	Food
Lucanidae	750	Dead trees, logs, stumps	Decaying wood
Passalidae	490	Under bark of dead trees, logs	Decaying wood
Geotrupidae	300	Soil, often in excavations below dung	Dung, fungi, green and decaying vegetation
Acanthoceridae	120	? Under bark, in litter, soil	? Decaying vegetation
Trogidae	167	Soil below dry vertebrate carcasses	Carrion
Scarabaeidae			
Aclopininae	14	?	?
Hybosorininae	100	Ground layer	Carrion
Aphodiinae <sup>1</sup>	1,220	Dung, or burrows in soil	Dung, green vegetation at night, ? roots
Scarabaeinae	2,000	Soil below dung	Dung
Melolonthinae	9,000	Soil	Roots, organic matter
Rutelinae	2,500	Soil	Roots, organic matter
Dynastinae	1,400	Soil, logs	Roots, organic matter
Valginae	200	? Associated with termites	
Cetoniinae	2,600	Soil, humus	Organic matter

<sup>1</sup> Including Aegialinae

subtropics, to numerous smaller families of small beetles, many of which probably have very specialised relationships with micro-organisms.

Even if attention is restricted to Group 4 in Table 1 there still remains the majority of the larger families of Coleoptera, *i.e.*, six families of 7,000 to 60,000 known species. Apart from their mechanical effects on soils they are important as predators of other soil animals, or as feeders on roots, dead plant material and/or associated microbial biomass. The Carabidae, which have been mentioned, are predominantly predators and scavengers while the larvae of many if not most Elateridae are root-feeders. Although Cerambycidae, Chrysomelidae and Curculionidae are all typically phytophagous above the soil surface, the Cerambycidae and Curculionidae (the largest family of animals) contain root-feeding species. In the Chrysomelidae, larvae of Eumolpinae and Cryptocephalinae are found in the soil and, they probably feed on roots as well.

Finally the Scarabaeidae and other families in the Scarabaeoidea exemplify a single major phylogenetic radiation which contributes to the soil, and to the soil system as a whole, in a variety of different ways. The larvae live almost exclusively in soil and allied habitats (Table 2) and occupy a low position in the trophic system, feeding mainly on live and dead plant material and associated micro-organisms. Adult scarabaeoids are large bulky beetles, up to 7.5 cm or

more in length and the group includes some of the largest of all insects. They can occur at very high population densities, for example around 400 scarabaeids per square metre in Australian and New Zealand grasslands. Without entering into the extensive literature on their population dynamics and pest status, it can be noted that Scarabaeidae in particular can have important influences on soil properties and processes. Over much of the Old World tropics and subtropics they also have a very significant role in nutrient cycling by disposing of large quantities of dung produced by herbivorous mammals (Bornemissza, 1961). This may be consumed by the larvae on the soil surface or in burrows excavated and stocked by the parent beetles.

The question of the food of larval scarabaeoids typifies a recurrent problem in soil zoology: to distinguish between what is ingested and what is digested. Scarabaeid larvae for instance commonly ingest live and dead roots, soil organic matter, mineral particles of the rhizosphere and other micro-organisms; for any one scarabaeid species it may be difficult to establish on what elements of this intake larval nutrition actually depends (Greenslade and Greenslade, 1983). This is complicated by the existence of a continuum, in the Scarabaeidae for example, from Cetoniinae whose larvae feed on organic matter, to Rutelinae and Melolonthinae feeding on live roots. The digestive physiology of scarabaeoid larvae is an important topic which is beyond the scope of this paper but, clearly, the group as a whole is one which merits much more attention from the point of view of their effect on the soil system (see Table 3 below).

### PEDOLOGICAL INFLUENCES OF SOIL PTERYGOTA

Hole (1981) discussed 11 different ways in which animals can affect soils citing many examples, with references, that involve insects. They need not be repeated here in detail but three groups are briefly examined (Table 3).

Merely by excavating galleries and burrows in soil all three of the taxa in Table 3 contribute to effects 1, 2, 4 and 6. Humphreys and Mitchell (1983) suggest that mixing by soil animals may have a significant effect on the rate of development of texture contrast soil profiles; they point out that, over time, it allows rainfall to affect a greater thickness of the profile than just the surface. Ants and termites backfill voids (effect 3) when they remodel their nests or when those structures are taken over and altered by other ant or termite species, and soil-living scarabaeid larvae generally fill their burrows behind them. Soil erosion (effect 5) is influenced by removal of plant-cover (*e.g.*, by scarabaeoid larvae) and by deposition of loose soil on the surface, susceptible to movement by wind or water, when subterranean nests are initially excavated or when they are cleaned (*e.g.*, by ants). Elevated ant and termite mounds with a cemented surface or matrix, or a protective gravel cover can reduce erosion locally but may accelerate it elsewhere by modifying surface run-off of rain water.

Because of their population biomass and their food, ranging from dry dead wood to already well-decomposed organic matter, both termites and scarabaeoids have important influences in regulating the nature and mass of plant litter, and the course and rate of decomposition and hence nutrient cycling (effects 7 and 9). Termites can accelerate processes by disposing of recalcitrant substances with a high content of lignin, or retard them by locking up material in long-lasting nest structures (Lee and Wood, 1971). Ants have minor effects here although those with large thatched mounds, for example some wood ants, *Formica* spp. in the northern hemisphere, and the myrmicine *Myremecia pilosula* in Australia, have some effect on the distribution of litter. However, Cowan *et al.* (1985) concluded that the Australian *Camponotus intrepidus* which also has thatched mounds, has a trivial role in pedogenesis. Ants very rapidly

TABLE 3. Pedological effects of soil fauna, from Hole (1981), and the roles of the pterygote insects: termites, ants and scarabaeoid beetles.

Effect	Taxon		
	Termites	Ants	Scarabaeoids
1. Mixing	+	+	+
2. Forming voids	+	+	+
3. Backfilling voids	+	+	+
4. Forming and destroying peds	+	+	+
5. Regulating soil erosion	+	+	+
6. Regulating movement of water and air in soil	+	+	+
7. Regulating plant litter	+	(+)	+
8. Regulating animal litter	+	+	+
9. Regulating nutrient cycling	+	(+)	+
10. Regulating biota	-	+	+
11. Producing special constituents	+	+	+

recycle any invertebrate carrion that appears on the soil surface (effect 9) usually finding it within minutes of its arrival, but this cannot compare with the mass effect of termites and beetles (such as scarabaeoids) on plant material.

Termites seem to have little direct influence on other biota (effect 10), excluding their microbial gut flora and the animals, mainly insects, that live with them in their nests. Indeed much of the success of the order Isoptera must derive from their exploitation of resources that were hardly used by other animals. In contrast, ants are particularly significant as dominant predators and competitors on the soil surface and in litter, with profound effects on the rest of the soil and surface fauna at both ecological and evolutionary levels. Soil-living scarabaeoids perhaps illustrate the classic influences of soil fauna (according to conventional wisdom) in comminuting plant material, dispersing soil micro-organisms and controlling their populations by feeding upon them.

All three taxa have the final effect (11) of producing special constituents. Both ants and termites make structures from selected soil particles, frequently cemented with salivary secretions or faecal material, while scarabaeoid larvae leave excreta-filled tunnels behind them.

Three effects of soil insects do not come across clearly in Hole's scheme. They are effects: (1), on the rhizosphere (*e.g.*, by scarabaeoid larvae); (2), of soil-nesting and mound-building ants and termites on the distribution pattern of plant nutrients in the horizontal plane; and (3), on the composition and structure of A-horizons (although to some extent the last is covered by Hole's 'mixing' or 'bioturbation').

The interactions of termites with soils were reviewed by Lee and Wood (1971). They showed that two of the most important activities of species that build mounds are the concentration, in the mounds, of organic matter and hence plant nutrients, and the elevation of lower horizon



material to the surface. More recently, Holt *et al.* (1980) and Spain *et al.* (1983) have studied the pedological significance of mound-building termites in northern Australia and their results are typical of those in the literature. On two soil types (red and yellow earths) Holt *et al.* (1980) found a total mound basal area of about 1% of their plots. Assuming the life-time of a mound from inception to complete erosion to be 25–50 years, they calculated an annual rate of accumulation of lower horizon soil on the surface of 0.025–0.05 mm per year. This means that any point in the landscape will support a termite mound once every 1–1,000 years and that in the 10,000 years since the end of the Pleistocene a 20–50 cm thick uppermost horizon could develop from the erosion of termite mounds. Since termite galleries commonly extend 1–2 m into the soil it follows also that over a few millennia entire soil profiles, or all of the upper part, can be worked and reworked by termites. In this way, termites appear to have a major role in the formation of the tubulo-alveolar laterites and pisolitic laterites and bauxites that are frequent throughout the warmer parts of the world. From the micromorphology of these laterites and bauxites, and their content of plant and termite fragments, de Barros Machado (1982a, b) concluded that they are formed by capillary impregnation by sesquioxides of the lining of termite galleries.

Mound-building ants also have received considerable attention on account of their possible role in raising soil to the surface and in affecting the distribution of plant nutrients, recently for example from Briese (1982), Cowan *et al.* (1985), Culver and Beattie (1983), Davidson and Morton (1981), Humphreys and Mitchell (1983) and Mandel and Sorenson (1982) and these authors provide many references to earlier investigations. Most of this work however has been done outside the tropics (in which ants reach their greatest diversity) and has generally involved only one or a few ant species which construct distinct nest mounds.

Humphreys and Mitchell (1983) recognised two broad types of mound, Type I where subsoil material is simply deposited loosely on the surface and Type II in which the mound is chambered, and the material compacted and cemented, to form a much more permanent nest structure. In fact there is a continuous range of nest types from subterranean nests that just open on to the soil surface, to entrances that are surrounded by fans, rings or small turrets of loose soil, through mounds that are increasingly compacted, worked and variously covered with thatch or gravel, to some very elaborate structures. Examples are the nests of New World fungus-growing ants (*Attini*), described by Moser (1963) and Weber (1966) (and see Wilson, 1971), and the ring nests of certain *Polyrachis* species on red earths and earthy sands in central Australia. The latter, which have yet to be described in detail, consist of substantial earthen rings which are covered with dead leaves of mulga (*Acacia aneura*) and contain a complex arrangement of interpenetrating galleries and spouts opening into voluminous atria.

These mound structures have a variety of functions ranging from spoil heaps or middens, to the control of nest microclimate and flood-defence. When they are thatched or covered with gravel the covering may act as a protection against rain splash erosion (Cowan *et al.*, 1985) and/or as a behavioural boundary (Gordon, 1984).

For some species the longevity of these mounds, for example the large gravel-covered nests of the meat ant, *Iridomyrmex purpureus*, of eastern Australia, is such that their contribution to pedogenesis is negligible, despite their size (Greenslade, 1974; Cowan *et al.*, 1985). In other species, however, the turnover rate is much more rapid and Culver and Beattie (1983) cite King and Sallee's (1956) and Smallwood's (1982) observations that the half life of large *Formica* mounds may be 10 years or less while some species relocate their nests several times a year. In arid Australia there are indications that nest turnover, even for the elaborate ring nests of

*Polyrachis* species, is very much more rapid than was hitherto assumed (P.J.M. Greenslade and W.A. Low, E. and B. Case, unpublished observations). It has been estimated that subsoil is brought to the surface by ants at rates of up to 0.1 mm per year, for example by *Formica cinerea* in North America (Baxter and Hole, 1967), quite comparable with estimates obtained for termites. These rates are of a magnitude that could be a significant influence in pedogenesis within the time-span of the Holocene so that it becomes unnecessary to extrapolate over longer periods of time that include major climatic changes and probable changes in the rate and nature of biological activities in the soil. Humphreys and Mitchell (1983) point out that, depending on soil material, rate and depth of mixing, and intensity of rainfall and rainwash, animal activity in general (including that of ants and termites) can either homogenize soil profiles or accentuate texture contrasts, leading to duplex profiles.

In semi-arid southern Australia Briese (1982) studied the combined effects of the members of a moderately diverse assemblage of ants. There was a total of 22 species in a plot of 500m<sup>2</sup> of low, open chenopod shrubland and none of them built large mounds. The turnover rate of soil attributed to these ants was 0.03 mm a year, again comparable to figures for termites in northern Australia.

Several investigators have compared the properties of mound and nonmound soils [see for example Culver and Beattie (1983), Davidson and Morton (1981a, b) Mandel and Sorenson (1982)]. They found commonly, but not invariably, enhanced levels of plant nutrients in the mound soils, notably of nitrogen and available phosphorus and, where ants allow plants to grow on mounds, floristic contrasts with surrounding areas. Briese (1982) compared soils from the nests of six selected ant species with those from control sites. Four seed-harvester or seed-harvester-omnivore species and one predator showed increased concentrations of nitrogen and phosphorus in nest over control soils, especially close to the surface. This was related to the presence of discarded prey fragments, seed husks and other plant material. However, a non-harvesting ant, an *Iridomyrmex* species which is a predator-omnivore, does not discard material around the nest entrance, and there was no nest-enhancement of plant nutrient concentrations. Levels actually decreased, probably because of the presence of lower horizon material that had been brought to the surface.

Charley (1971) and Rixon (1970) have described and discussed the significance of the surface patterning of plant nutrients in the type of shrubland in which Briese studied ants. Briese added the point that, by concentrating nutrients around their nest entrances, ants contribute to a mineral mosaic which influences the overall nutrition of the plant community. This can be extended to other soil-nesting ants and termites. The scale at which they are likely to influence nutrient patterns is close to that illustrated by Tillman (1982), who argued that adaptation to and competition for specific ratios of resources, such as nutrients, is a major factor in the coexistence of plant species and in the control of floristic diversity. Consequently, the effects of social insects on soils may have wide significance to vegetation.

Briese's (1982) work takes us back to the problems created by insect diversity. First, when ant communities are composed of large numbers of species (as is the rule over most of Australia for example, and the whole of the world's tropical regions) with differing effects on the soil, the influence of each species should be assessed independently. When a local ant fauna can consist of more than 100 species in an area of less than 1 ha, the difficulties are obvious. Second, there is the problem of identifying the species, essential if one study is to be comparable with another.



Fig. 1. Relative apparent taxonomic knowledge of soil Pterygota, from 1, probably very inadequate for most groups, to 6, good, more than 90% of species described, at least as adults, in most groups.

### IDENTIFICATION OF SOIL INSECTS

The accurate identification of species is essential to any biological study in order to allow the comparison, application and testing of results, just as the consistent and accurate identification of soil types is essential to any study of soils. Hollis (1980) has edited a multi-authored guide aiming to provide a list of primary references, enabling non-specialists to set about identifying insects, including soil pterygotes, from any part of the world. Because of the diversity of soil biota, however, and especially of soil insects, specific identification often seems to be an ideal the attainment of which is surrounded by insuperable barriers. In many studies, specific identification is sacrificed for the sake of statistical validity, and animals identified only to the level of the family or even the order, a pronounced deficiency of much research in soil zoology.

Australian ants illustrate the sort of problem that the identification of insect species presents to the soil zoologist. To take only one example, Bolton (1981) revised the African members of the ant genus *Meranoplus* which is distributed through the Old World tropics and adjacent areas. From the taxonomic literature, he concluded that the Australian region had the most diverse fauna with *ca.* 25 named taxa. Since 1970, I have collected more than 200 *Meranoplus* species in Australia and this can be but a fraction of the total so that less, and probably much less, than 10% are described. Consequently, for this quite important genus there are hardly any descriptions of species, no keys for their identification and its study is closed to the non-specialist. Admittedly, the Australian ant fauna is remarkably diverse; but in other continental areas other groups of soil insects have radiated in the same way, creating the same obstacles to research.

New (1984) refers to this as the 'taxonomic impediment' to work on insects. The problem was discussed by Wilson (1980) who considered it capable of being solved. He started with the then commonly agreed maximum figure of a total of 10 million species of organisms of which *ca.* 1.5 million had been described. He suggested that if a taxonomist deals with 10 species per

year over a span of 40 years, 25,000 taxonomists' working lives would be required to revise the biota of the world, a not impossible number given contemporary populations of scientists. However, basing calculations on the number of host-specific Coleoptera on tropical trees, Erwin (1982) proposed that there may be up to 30 million species of tropical arthropods. New (1984) describes "reactions ranging from incredulity to relief that a more realistic figure has been published." It is unlikely that many soil zoologists acquainted with the invertebrate fauna of the litter layer in lowland tropical rain-forests would dispute Erwin's estimate, even if they disagreed with the means by which he arrived at it. Indeed it is quite probable that an extensive survey of ground-layer invertebrates in tropical rain-forests would result in another massive increase to the estimated total. It should be added that this figure refers to taxonomist's morphological species and evades the question of species that can be recognised only with the biochemical and karyological techniques of the geneticist.

The taxonomic problem is not uniformly spread throughout the different groups of soil insects or the world's geographical regions. Some insects that are important in the soil system are relatively well known, even in the tropics. The prime example is the Isoptera (termites) although even here much taxonomic study is still needed. At the other extreme lie groups such as tropical curculionid and staphylinid beetles. There have been a number of attempts to assess the state of taxonomic knowledge of selected portions of the biota. Examples are surveys of recorded, and estimates of the uncollected, soil fauna of Canada (Danks, 1979; Marshall *et al.*, 1982); terrestrial and freshwater Hexapoda (*i.e.*, pterygote and apterygote insects and allied groups); Myriapoda and Arachnida of New Zealand (Watt, 1983); insects of Australia (Taylor, 1976); and biota of the British Isles with particular references to insects (Stubbs, 1982). Figure 1 is a very subjective attempt to illustrate geographical variation in the apparent magnitude of the taxonomic impediment to work on the pterygote of the soil insects. It derives from surveys such as those mentioned, superficial familiarity with the taxonomic literature and the impression gained from collecting and sampling a variety of soil insects in the world's major biomes. Regional variation is caused by such factors as differences in the diversity of faunas and in the history of biological investigation in different areas.

By far, the best known soil insects are those of Britain and northwestern Europe, where probably more than 95% of species are described and a comprehensive range of guides and keys to adults is available. Even here, however, the specific identification of immature stages is generally difficult and impossible for many taxa. In New Zealand, more than half the species are thought to be described, while in Australia, it is estimated that more than half have yet to be collected. In the humid tropics, of course, the situation is much worse, but precisely how much we do not know.

Much current taxonomic work is based on revisions of genera, in which all available representatives of a genus are gathered together and species are described or redescribed and catalogued. It is then possible to revise the higher classification and to prepare keys to species. For most of the world's soil pterygotes it is obvious that this conventional taxonomic process is quite inadequate. For example, of the postulated 30 million or so arthropod species about 12 million or 40% should be Coleoptera. At the current rate at which Coleoptera species are being described (*ca.* 2–3,000 per year, see account of Coleoptera here) a very long time indeed would elapse before all were known. Unsatisfactory partial answers are available in that attention can be restricted to better known taxa and/or the soil zoologist can become his own taxonomist. Sometimes species can be identified through a combination of voucher specimens and code numbers, but this system fails in large, inadequately known genera. A possible solution lies in

inverting conventional taxonomy. Instead of starting with the description of species, work should proceed downward from higher taxonomic categories in order to provide guides to genera and, within large genera, to natural groups of species. In this way, the material with which the soil zoologist works is reduced to sets of species of manageable size that are relatively easily recognised and when recognised convey biological information. It is feasible also to link species' identities to vouchers and code numbers. The time-consuming production of detailed species-descriptions, which generally fail to discriminate between sibling or cryptic species, and are rarely adequate without access to types, can probably be omitted. At least it can be deferred, carried out on a provisional basis or concentrated on critical groups of species.

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